The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland.

Craig L. STRONG[1]

Sarah L. BOULTER[2]

Melinda J. LAIDLAW[3]

Sarah C. MAUNSELL[2]

David PUTLAND[4]

Roger L. KITCHING[2]

1. Atmospheric Environment Research Centre, Griffith School of Environment, Griffith University, Nathan Qld 4111 Australia; 2. Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email: s.boulter@griffith.edu.au; 3. Queensland Herbarium, Biodiversity and Ecosystem Sciences, Department of Environment and Resource Management, Toowong Qld 4066, Australia. 4. Growcom, PO Box 202 Fortitude Valley Qld 4006, Australia

ABSTRACT

Climate and soil properties are key factors influencing vegetation and biota. As such, an understanding of the variability in climate and soil properties along an altitudinal gradient can be used to explain changes in vegetation and biota along the same gradient. Understanding these patterns can offer a powerful predictive tool with respect to changes in climate. The temperature, relative humidity and wind speed and direction were logged throughout the day and night for up to 333 days continuously at five different altitudes in the subtropical rainforest of Lamington National Park, Queensland, Australia. In addition, soil sampling was carried out at the same sites and elements of the physical, chemical and mineralogical characteristics of the soil tested. Temperature decreased with increased altitude, although less temperature variability was experienced at higher altitudes. All sites experienced relative humidity close to 100% for most nights throughout the year, although daily temperature increases reduced humidity at most sites. Increasing windiness at the highest (1100 m above sea level (a.s.l.)) altitude reflected meso-scale synoptic conditions. Soils demonstrated increasing moisture, organic matter and acidity as elevation increased. The macro- and micro-nutrients measured showed variable responses with nitrogen increasing and the other macro-nutrients decreasing with altitude. Aluminium increased exponentially with altitude. Moisture and temperature appear to be important drivers in soil parameters and therefore biological patterning along the transect. Future climate change resulting in atmospheric warming and drying are predicted to have a significant impact on moisture availability both in the canopy and soil environments. ☐ *altitudinal gradient, subtropical rainforest, microclimate, soils.*

Many insect and plant species are distributed along an altitudinal gradient, partially reflecting the changes in local climate. The main changes

observed in local climate along an altitudinal gradient involve changes in temperature, precipitation, humidity, wind speed and radiation (Barry 1992). The study of an altitudinal gradient therefore offers an alternative to experimentation when investigating long-term climate change (e.g. Williams *et al.* 2003, Hodkinson 2005, Chen *et al.* 2009). The predictable changes in abiotic conditions offer an opportunity to detect associated biotic patterns and, when matched with the predicted changes in physical parameters associated with climate change, offer a powerful predictive tool.

IBISCA, an international research programme, aims at studying the spatial (horizontal, vertical, altitudinal) and temporal distribution of arthropods and their interactions with plants and other selected organisms. The IBISCA-Queensland Project (Kitching *et al.* 2011) specifically explored the diversity of arthropods, plants and fungi from the soil to the rainforest canopy along an altitudinal transect in Lamington National Park, Australia, for the purpose of assessing and predicting the impact of climate change on biodiversity. Predicting biological changes along an altitudinal gradient also requires study of the edaphic conditions, as individual sites will experience considerable variability as a result of the interaction between topography, slope, aspect and meso-scale synoptic conditions (Proctor *et al.* 2007, Bendix *et al.* 2008, Wilcke *et al.* 2008, Gerold *et al.* 2008). In order to better quantify the climatic and physical changes associated with the different IBISCA-Queensland plots and altitudes, a programme of micrometeorological monitoring and a simple soil sampling scheme were devised. The aim of this paper is to describe the micrometeorological properties and soil characteristics associated with an 800 metre altitudinal gradient at Lamington National Park, Queensland, Australia. These findings provide an abiotic context to other IBISCA-Queensland research projects so that they may assess and predict the patterns of their focus taxa along the altitudinal gradient.

MATERIALS AND METHODS

Study site. The IBISCA-Queensland Project was conducted in the subtropical rainforest of Lamington National Park (28° 13′ S 153° 08′E). The project established 20 permanent plots, across five broad altitudes; 300, 500, 700, 900 and 1100 m above sea level (a.s.l.). Each altitude had four replicated plots (A–D) spaced a minimum of 400 m apart. Plot selection was determined according to a hierarchy:

1. appropriate altitude;
2. all plots had to be within the same water catchment, West Canungra Creek; and
3. all plots had to be accessible to researchers carrying equipment on foot.

All plots had a 20 m x 20 m quadrant pegged out and a centrally positioned permanent metal post. This quadrant was the location for all baseline sampling for vegetation and arthropods (see Kitching *et al.* 2011). In addition, some projects also conducted sampling within a 50 m radius of the central metal post. A full description of the project rationale and scope are discussed in Kitching *et al.* (2011).

Geology and climate. Lamington National Park is located on the McPherson Range and associated spurs that form the northern flanks of the Mt Warning erosion caldera. The caldera is the largest and best preserved basaltic shield volcano in Australia (Willmott 2004) and is all that remains of a broad shield volcano which erupted between 24 and 20 million years ago (Graham 2001). Being on the northern section of the caldera, the study sites are dominated by rocks of the Tertiary Lamington Volcanics (Morand 1996). Three major periods of volcanic activity over a four million year lifespan have resulted in a complex banded geology. Beechmont Basalt is overlain by Binna Burra Rhyolite and scattered pyroclastic vents, and capped by younger Hobwee Basalt (Stevens 1976). Basalts in the region vary from fine-grained to textured dolerites and porphyritic

basalts and can be vasicular, scoriaceus or amygdaloidal (Morand 1996).

The subtle differences in basalt chemical composition, differential weathering characters and age of weathering surfaces, in conjunction with varied topography and the resulting microclimate has resulted in a wide variety of soil types (Beckmann & Thompson 1976). Contemporary erosional processes continue today, exposing fresh surfaces and depositing fresh alluvium. The alluvium is high in basalt derived clay and contains the products of both recent and historic weathering (Beckmann & Thompson 1976). Across the caldera, basalts on the plateaus generally weather to krasnozem soils while those on the slopes can form poorer lithosols (Beckmann & Thompson 1976).

Climate in the study region is driven by the movement of high and low pressure systems from the west, producing strong seasonal patterns (McDonald & Whiteman 1979). A pronounced wet season occurs during the austral summer driven by low pressure systems and tropical cyclonic depressions (Morand 1996). Almost thirty percent of annual precipitation falls between February and March while only seven percent is received between August and September. Moisture laden onshore winds are orographically lifted as they meet the McPherson Range, producing highly erosional rainfall particularly at the highest elevations. Rainfall is supplemented at higher elevations by low cloud and fog (Morand 1996). Evapotranspiration rates at Murwillumbah, located on the coastal side of the caldera, peak in December (5.3 mm/day) and are at a minimum in June/July (1.7 mm/day) (Morand 1996). The dry season, from winter to spring, is characterised by dry, westerly winds associated with the passage of cold fronts and by calm conditions associated with large stable high pressure systems (McDonald & Whiteman 1979). Under calm conditions frosts are common but their frequency and intensity is greatly affected by topography (McDonald & Whiteman 1979). The mountainous terrain produces innumerable

microclimates linked with both coarse and fine scale changes in altitude, aspect and slope.

Microclimate. An automatic weather station (La Crosse WS-3600 Weather Pro, La Crosse Technology Ltd, USA.) was installed at each altitude. The station was positioned on the perimeter of the permanent 20 m x 20 m quadrats at sites 300D, 500A, 700A, 900A, 1100B. Weather parameters measured included temperature, relative humidity, rainfall, atmospheric pressure, dewpoint temperature, wind speed and wind direction. All parameters were measured at a height of 1.5 m a.s.l., except rainfall which was measured at ground level. The weather stations recorded data every thirty minutes from October 2006 until February 2008. However, the fine electronics of the tipping bucket rain gauge failed to operate at all sites due to high moisture conditions and insect activity associated with the forest floor. Instead, rainfall data was derived from two Bureau of Meteorology rainfall stations. At an altitude of 100 m, the Finch Road Canungra station (BoM Station Number 40042; 28.01°S, 153.17°E) is located 17 km downstream from the 300 m altitude plots and operated from 1916 to 2008. At an altitude of 917 m, the Green Mountains station (BoM Station number 40182; 28.23°S, 153.14°E) is located in very close proximity to the 900 m plots and has operated from 1916 to the present. The long-term rainfall record (greater than 90 years) at the two altitudes (900 m and 300 m), whilst not providing data from the IBISCA plots, does give an overview of the differences between altitudes.

A temperature and humidity data logger (LogTag ™ HAXO-8, LogTag Recorders Ltd., Auckland, New Zealand) was installed at both the understorey and canopy levels on each of the 20 plots to increase the spatial monitoring of these important parameters. The data loggers recorded temperature and humidity every 60 minutes with a memory capacity of 333 days. Loggers in the understorey were attached to the centre post of each plot at 1.5

m a.s.l. and sampled between July 2007 and mid June 2008. Loggers in the canopy were suspended in the upper (but not outermost) canopy, as close as possible to directly above the centre post. Installation of the canopy loggers was more difficult and therefore occurred over a two week period from late September to early October 2007 with the units running for 333 days up until early October 2008. As the height of the canopy varied between altitudes (35 m at 300 m a.s.l. and 25 m at 1100 m a.s.l.) the height of the loggers also varied, but importantly the measurements represented the local canopy microclimate. They were installed without any environmental enclosure (e.g. Stevenson screen) affecting, at times, the quality of data. For example, occasional canopy temperatures at one plot will be 10 degrees higher than any other plot at the same altitude at the same time. We assumed that this resulted from direct exposure to the sun and have excluded any such outliers in our analyses.

Soil. A single set of soil samples was collected from each of the 20 plots between March 11-14, 2008. Sampling occurred two weeks after widespread regional rainfall. Five samples were taken randomly within each plot by first scraping aside all leaf litter and surface organic matter and obtaining a 6 cm by 6 cm by 15 cm deep core. The five cores from a plot were then thoroughly mixed and a sub-sample extracted to represent each plot. A range of soil chemical analyses were carried out by Phosyn Analytical Pty Ltd (Andrews, Queensland) with all extraction protocols following those outlined in Rayment and Higginson (1992). Soil pH was analysed potentiometrically, in both 0.01 M $CaCl_2$ and water, using a soil-dilutant ratio of 1:5. Organic matter percentage was determined from loss on ignition (360°C for 2 hours). Cation exchange capacity (CEC) was derived by calculation. Electrical conductivity (EC) was analysed potentiometrically via a soil-water ratio of 1:5. Ammonium (NH_4^+-N) and nitrate (NO_3^--N) were extracted with water and

analysed with segmented flow analysis. Trace elements sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg) were extracted with ammonium acetate and analysed with inductively coupled plasma atomic emission spectrometry (ICPAES). Copper (Cu), zinc (Zn), manganese (Mn) and iron (Fe) were extracted with diethylenetriaminepentaacetic acid (DTPA) and analysed using inductively coupled plasma atomic emission spectrometry (ICPAES). Aluminium (Al) was extracted with potassium chloride (KCl), sulphur(S) in MCP and chloride (Cl) in water. All were analysed with ICPAES. Phosphorus (P) was analysed following the Olsen-extraction technique determination via spectroscopy. A low resolution texture analysis was conducted by hand texturing and colour was determined using Munsell colour notation on dry samples.

Additional temporal measurements of soil moisture were made by one of us (SM) at three of the altitudes 700, 900 and 1100 m a.s.l.. Sampling was undertaken every two to three months between August 2008 and April 2009 at all four plots at each of the three altitudes. Sampling across the altitudes occurred in a two to three day period with the exception of the 700D sample in October 2008 which could not be accessed for ten days due to logistical problems and therefore this sample was excluded from analysis. Five sub-samples of soil were taken from each plot on each sampling occasion. Leaf litter was first removed and then twenty-five to thirty grams of soil (to 8 cm deep) was collected with a trowel and transferred to pre-weighed soil moisture tins. The percentage of moisture in each sub-sample of soil was measured using the gravimetric method (Rayment & Higginson 1992) and then averaged across the five sub-samples.

The means of all soil parameters (except texture and soil colour) were compared across altitudes using one-way ANOVA. A two-way repeated-measures ANOVA was used to test for differences in temporal soil moisture data; the two independent variables in the model
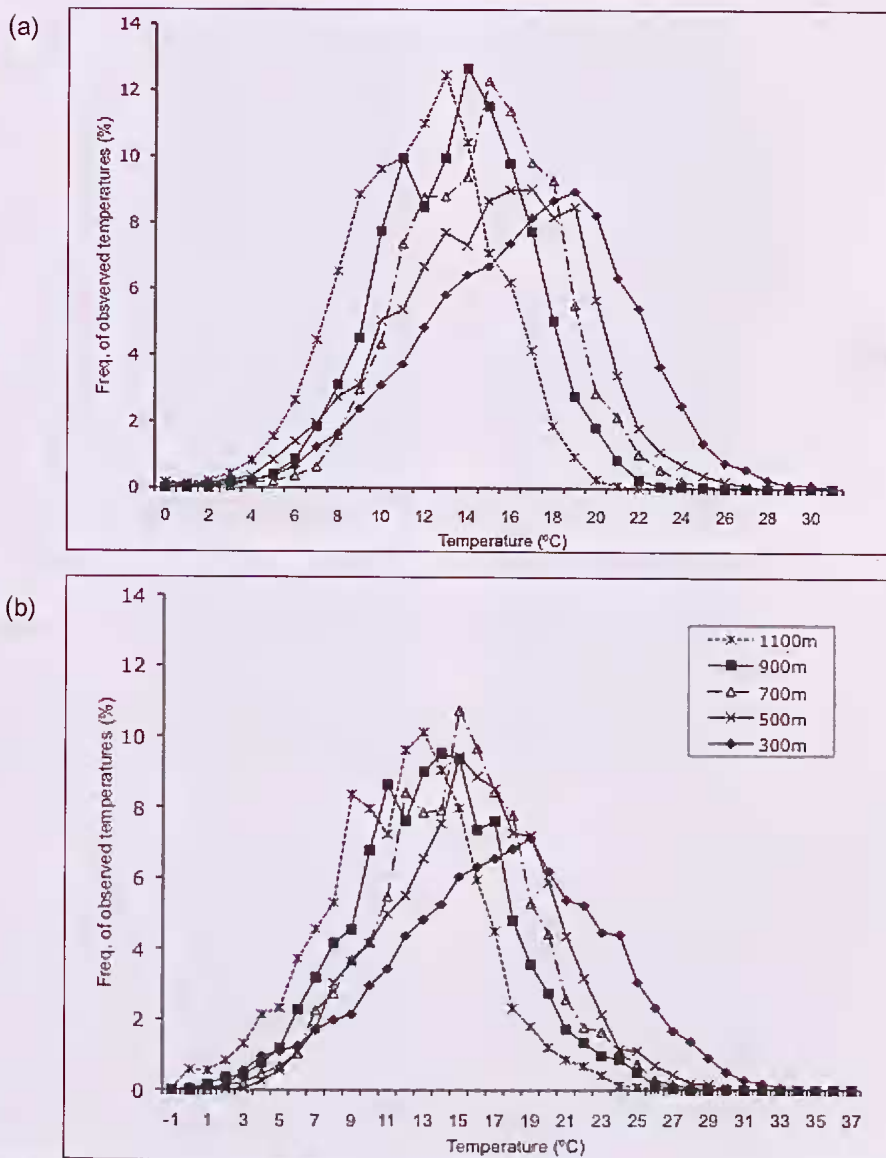
FIG. 1. Frequency (percent) of temperatures averaged across four plots at each of five altitudes in the rainforest, a) canopy and; b) understorey of Lamington National Park. Temperatures were recorded hourly across 333 days for each plot, across a range of dates from July 2007 to June 2008.

being time of year (month) and altitude. This more detailed statistical analysis of soil moisture acknowledges that measurements taken repeatedly through time on the same plots, could lead to the expectation that measure-ments taken closer together in time are more highly correlated than measurements taken further apart.
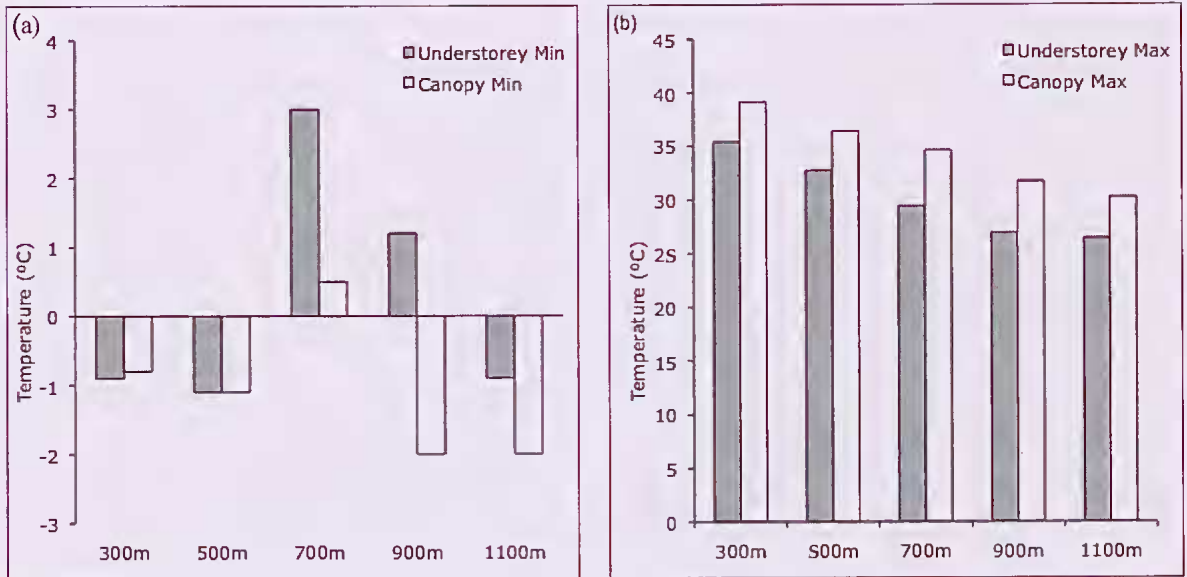
FIG. 2. Absolute (a) minimum temperatures and (b) maximum temperatures recorded in both the canopy and understorey across five altitudes recorded from July 2007 until August 2008.

RESULTS

Microclimate. The following results represent the first attempt at characterising micro-meteorological variations between small altitudinal increments of 200 metres at Lamington National Park. They provide general trends for temperature, relative humidity, wind speed and direction. Unfortunately, gaps in the data existed at all sites. Of the five weather stations, the 300 m had the most incomplete record with only 53% of observations successfully recorded. This particular location had access difficulties due to flooding and property management, prohibiting regular downloading of data and battery changes. Of the other four weather stations 73% of the data was collected at the altitude of 500 m altitude, 61% at 700 m a.s.l., 63% at 900 m a.s.l. and 73% at 1100 m a.s.l.. Greater continuity of recording was achieved using the data loggers. Hourly readings of temperature and humidity were obtained for all LogTag data loggers at all plots with the exception of those in the canopy at two of the 1100 m a.s.l. plots. Both of these

data loggers failed during the course of the 333 days of recording. Despite these limitations, the micro-meteorological results provide extremely useful insights into the abiotic drivers of ecological diversity.

Temperature. Both the median air temperature and the range in air temperatures decreased with increasing altitude. Expressed as frequency distributions, the median air temperature for both canopy and understorey become cooler as altitude increased (Fig. 1). Temperature differences (ΔT) between 300 m and 1100 m a.s.l. for both canopy and understorey were between 6 to 7°C, representing an average air temperature gradient (i.e. a decrease in temperature with increasing altitude) of 0.75 °C 100 m^{-1}. The range of temperatures experienced

FIG. 3. (Opposite page) Hourly temperature (°C) in the understorey (1.5 m above ground level) and canopy (25-35 m) of rainforest, averaged across four plots, at each of five altitudes along the IBISCA-Queensland gradient. Temperature was recorded by LogTag data loggers.

The physical environment in Lamington NP

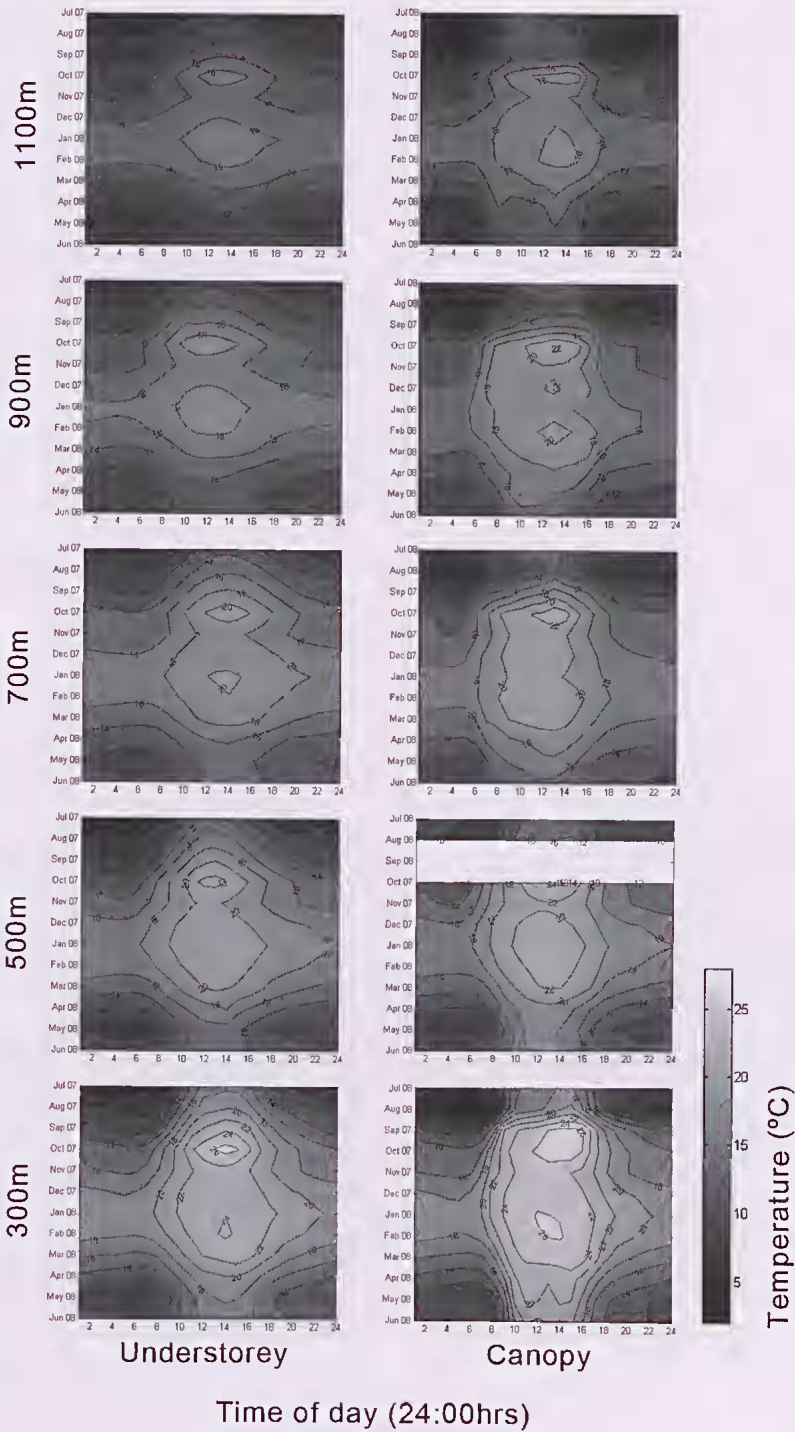Understorey   Canopy

Time of day (24:00hrs)

TABLE 1. Mean measurements of soil characteristics at each of five altitudes (four plots per altitude) along a gradient in Lamington National Park and their overall direction of change in relation to increasing altitude. S.E. in parenthesis after means. * indicates those variables that were significantly different between altitudes using one-way ANOVA, P<0.05. # indicates the trend was not strictly linear.

Soil Physical Parameter	Altitude					Direction of change with increased altitude
	300m	500m	700m	900m	1100m	
pH [H2O] *	6.4(0.14)	6(0.2)	5.425(0.39)	4.575(0.13)	4.325(0.06)	Decrease
pH [CaCl2] *	6.025(0.11)	5.625(0.17)	4.95(0.38)	4.15(0.12)	3.925(0.03)	Decrease
Organic Matter (%) *	12.05(1.01)	15.85(0.74)	14.95(0.75)	21.5(1.59)	27.175(2.23)	Increase
CEC (meq/100g) *	31.775(3.45)	29.65(2.19)	18.375(5.39)	7.975(0.94)	5.85(0.24)	Decrease
EC (dS/m)	0.1575(0.01)	0.165(0.01)	0.155(0.01)	0.125(0.01)	0.1275(0.004)	N/A
Ca base saturation (%) *	67.15(0.74)	70.95(4.67)	65.55(5.13)	46.3(10.58)	19.575(2.62)	Decrease
K base saturation (%) *	3.125(0.21)	2.475(0.09)	4.025(1.05)	5.75(0.29)	7.4(0.57)	Increase
Mg base saturation (%)	28.425(0.59)	25.125(4.23)	25.625(2.86)	22.5(4.06)	18.925(2.3)	N/A
Na base saturation (%) *	1.175(0.18)	1.2(0.34)	1.425(0.3)	2.4(0.16)	3.2(0.36)	Increase
Al base saturation (%) *	0.15(0.03)	0.25(0.03)	3.4(1.86)	23.075(14.04)	50.925(4.73)	Increase
Ca:Mg Ratio *	2.4(0.07)	3.15(0.66)	2.725(0.5)	1.975(0.26)	1.025(0.05)	Decrease #
Moisture (%) *	22.52(0.83)	26.24(0.98)	26.76(1.4)	33.55(1.81)	44.37(0.77)	Increase

at the 300 and 500 m a.s.l. plots were greater than those at the 700, 900 and 1100 m a.s.l. plots (Fig 1), with the 300 m a.s.l. plot experiencing a ΔT of up to 30°C (for the understorey) and a ΔT of 22°C at the highest altitude plot (Fig. 1).

The absolute maximum temperature also decreased with increasing altitude for both understorey and canopy level (Fig 2a). Absolute minimum temperatures, however, did not display a linear decrease, with the values at the two lowest altitudes less than those experienced at the 700 m a.s.l. sites. However, the absolute minimums were lower at the 1100 m a.s.l. compared to the 300 m a.s.l. plots (Fig. 2b). The canopy experienced colder minimums than the understorey for the three highest altitudes

(i.e. 700, 900 and 1100 m a.s.l.) (Fig. 2b). Across the five altitudes, understorey temperatures experienced ΔT values of up to 3°C less than canopy (Fig. 2b) and the difference between the absolute maximum and minimum temperature decreased with increasing altitude.

Diurnal and seasonal fluctuations in temperature were, as expected, experienced at all altitudes and in both the canopy and understorey (Fig. 3) over the sampling periods. The greatest difference in air temperature between the altitudes was experienced during day light hours (Fig. 3).

Relative humidity. Relative humidity clearly increased with altitude for both the understorey and canopy (Fig. 4). Diurnal and seasonal

TABLE 2. Mean measurements of soil nutrients at each of five altitudes (four plots per altitude) along a gradient in Lamington National Park and their overall direction of change in relation to inceasing altitude. S.E. in parenthesis after means. * indicates those variables that were significantly different between altitudes using one-way ANOVA, $P<0.05$. # indicates the trend was not strictly linear.

Soil Nutrients ~ Macro	Altitude					Direction of change with increased altitude
	300m	500m	700m	900m	1100m	
Macro nutrients						
Nitrate (ppm) *	9(1.98)	9.175(1.28)	15.2(3.33)	12.35(1.99)	20.5(3.48)	Increase
Ammonium (ppm) *	4.5(0.73)	5.525(1.08)	7.175(0.93)	9.375(1.02)	13.95(1.76)	Increase
Phosphorus (ppm)	31.75(4.71)	23.5(4.63)	19(1.68)	21.5(3.23)	21.25(2.29)	N/A
Potassium (ppm) *	381.25(40.99)	284.25(12.35)	229(40.03)	177(18.47)	168(8.64)	Decrease
Calcium (ppm) *	4270.5(477.91)	4268.5(556.27)	2551(873.55)	788.5(221.71)	232(41.24)	Decrease
Magnesium (ppm) *	1093.75(124.24)	869.75(80.49)	540.25(142.04)	227.5(55.65)	135.5(22.38)	Decrease
Micro nutrients						
Sulphur (ppm) *	12.25(0.48)	14.5(1.04)	20.25(3.77)	28.25(1.55)	29.75(2.29)	Increase
Boron (ppm) *	1.925(0.17)	1.575(0.28)	2.05(0.39)	1.125(0.13)	0.675(0.05)	Decrease
Copper (ppm)	1.325(0.19)	1.4(0.19)	1.825(0.26)	1.6(0.14)	1.05(0.09)	N/A
Iron (ppm) *	52.75(2.95)	66.75(3.57)	52.75(5.3)	69.5(8.19)	89.5(8.39)	Increase
Manganese (ppm) *	67.925(9.48)	55(3.1)	105.25(17.16)	69.65(20.33)	21.15(5.57)	Decrease #
Zinc (ppm) *	6.1(0.75)	4.4(0.36)	11.25(2.95)	1.825(0.32)	1.225(0.2)	Decrease #
Aluminium (ppm) *	3.75(0.48)	6.5(0.5)	30.25(12.59)	135(65.44)	264.75(17.56)	Increase
Sodium (ppm)	81.75(2.75)	75.75(14.23)	55(19.34)	43.25(2.95)	43.25(5.71)	N/A
Chloride (ppm) *	17.75(1.93)	16.25(1.03)	16.25(1.8)	22(0.91)	32.25(3.33)	Increase #

fluctuations in relative humidity were observed for all altitudes in both the understorey and canopy using the data loggers (Fig. 4). Humidities were highest during summer daytime, particularly at 1100 m elevation where the moist daytime conditions continued over a longer time period than all other altitudes. Relative humidity was higher in the understorey than in the canopy (Fig. 4). Relative humidity measured by the automatic weather stations from December 2006 – December 2007 showed similar diurnal and seasonal patterns (Fig. 5) with prolonged moisture levels both day and night also seen at the 1100 m a.s.l. plot.
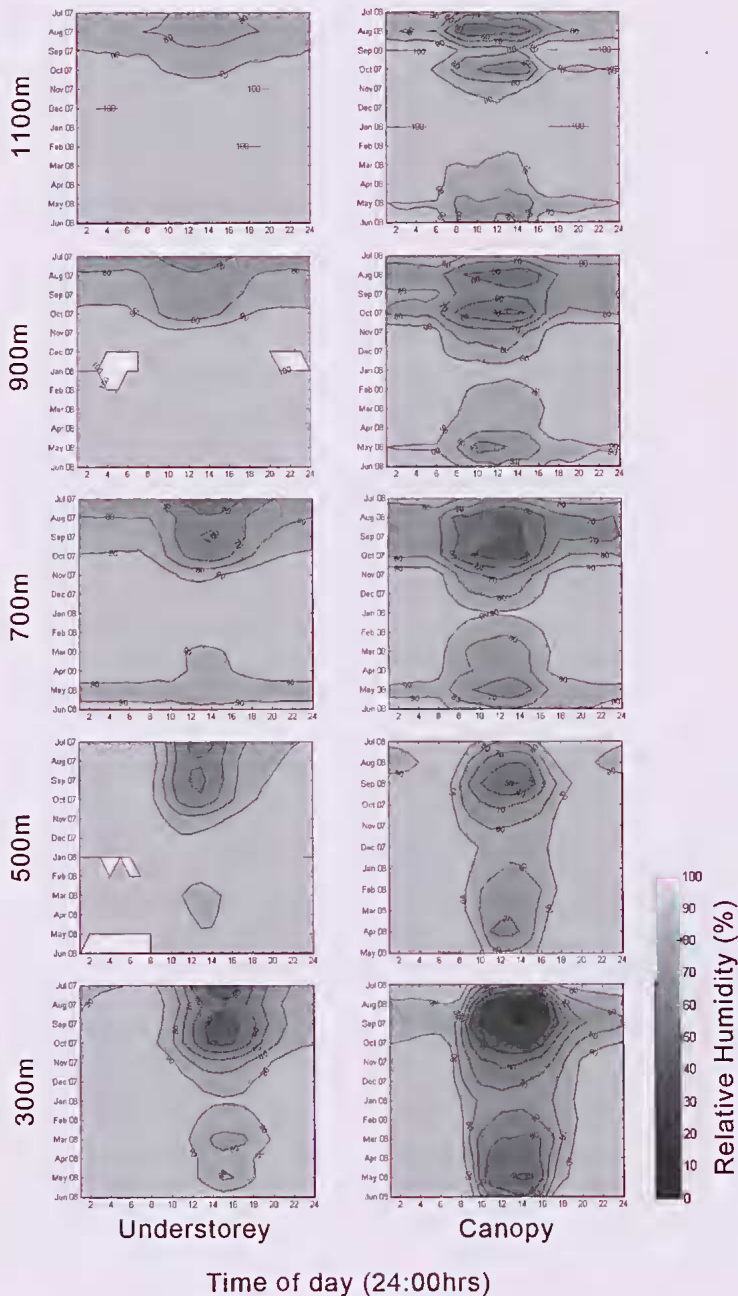
FIG. 4. Hourly relative humidity (%) in the understorey (1.5 m above ground level) and canopy (25-35 m) of rainforest, averaged across four plots, at each of five altitudes along the IBISCA-Queensland gradient. Relative humidity was recorded by LogTag data loggers.
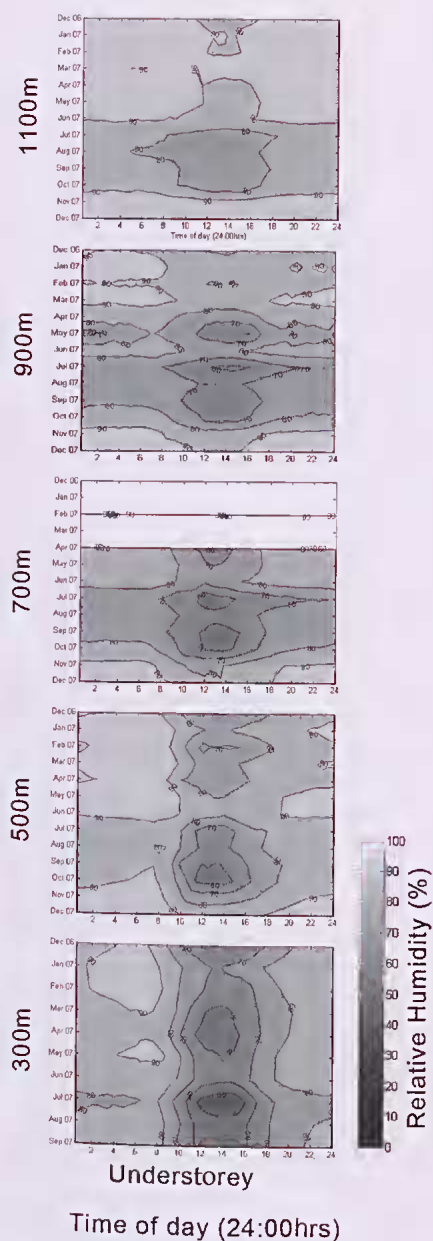
FIG. 5. Hourly relative humidity (%) measurements taken from five automatic weather stations, one at a plot within each of the five different altitudes, mounted approximately 1.5 m above ground level with readings averaged per month from December 2006 to December 2007.

Wind speed and direction. There was a clear increase in the incidence of wind with increasing altitude. Low altitude plots showed infrequent wind activity with wind speeds no more than gentle air movement (less than 2 m/s). In contrast, the 1100 m a.s.l. plot had frequent strong wind activity (greater than 12 m/s) (Fig. 6). Wind direction differed with altitude during the observation period with low altitudes experiencing predominantly north-easterly winds, clearly contrasting with the 1100 m a.s.l. plot where south-westerly winds prevailed.

Rainfall. Due to rainfall gauge failures, we consider here only the difference in rainfall at two altitudes – 900 m a.s.l. and 100 m a.s.l.- at Lamington National Park by utilising two long-term Bureau of Meteorology rainfall stations within the study catchment.

The long-term monthly rainfall averages over the past 92 years indicate the higher altitude rainfall location (917 m a.s.l.) receives on average, 21% more rainfall than the lower location (100 m a.s.l.), with the largest differences occurring in late summer and early winter (Fig. 7). Summer and early autumn is the dominant rainfall season, with late winter/early spring the driest at both altitudes. Comparing monthly totals between 2006 and 2008, we note that approximately 65% of monthly totals fell below the long-term average and that both within year and between year patterns between the two altitudes were generally similar, with the exception of extraordinarily higher rainfall totals at the 917 m weather station in January 2008 (Figs 8a, b).

Soil. Derived from Tertiary basaltic rocks, all plots had soils of loam to silty clay loam Krasnozem Gn4.11 or Gn4.12 in Northcote classification (Northcote 1979) and Ferralsol in FAO classification (FAO 1998). These Ferralsols have loamy textures with colours ranging from grey-browns at lower altitudes (300 and 500 m a.s.l.) and dark browns at the higher altitude plots (700, 900 and 1100 m a.s.l.). There were slight differences in topographic
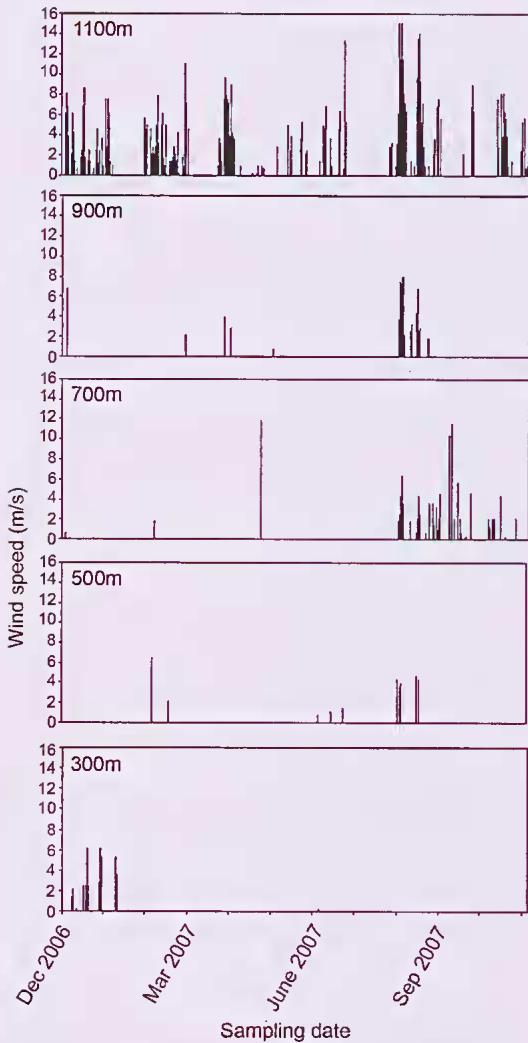
FIG. 6. Incidence of wind events at each of five altitudes between December 2007 and December 2007 as measured by automatic weather stations. Low altitude plots had infrequent, low wind speed events, while the 1100 m a.s.l. plot had stronger and more frequent events.

position between altitudes. The 300 m a.s.l. plots were positioned in the valley bottoms, partially on the flood plain of Canungra Creek. These plots had a southerly orientation and an average inclination of 10°. The 500 m

a.s.l. plots were on the lower mid slopes in close proximity to the high intensity zone of Canungra Creek. Orientation was southerly, with the exception of plot 500A, which was north-easterly, and slope angles averaged 10°. Positioned on the mid and upper slope, the 700 and 900 m a.s.l. plots were distant from Canungra Creek, instead situated in the vicinity of small gullies producing the upper tributaries of the catchment. These plots had a north-easterly orientation and average inclinations of 12° and 17° respectively. The 1100 m a.s.l. plots were located along a north-west to north-east facing ridge-line and had the greatest variation in slope of between 5° and 25° (average 14°). As some soil properties are known to vary because of slope processes, slope position should be considered when interpreting the soil data. The analysis presented here evaluates altitudinal variation alone.

Altitudinal variation of soil chemical parameters and texture. The chemical and physical analysis of the soil samples collected at all altitudes showed changes in almost all parameters measured along the transect (Tables 1, 2). Overall, the soils in the research area were acidic, with pH ranging from 6.0 to 3.9 and decreasing with altitude (Table 1). There was a clear increase in soil organic matter within the A horizon soils associated with increasing altitude (Table 1). The percentage of organic matter at the highest altitude was almost one third of the total soil, while at the 300 m a.s.l. sites, the organic matter constituted a little over 10% of the soil. The proportion of soil moisture almost doubled between the 300 m (mean = 22.52%) and the 1100 m (mean = 44.37%) sites, with a steady increase along the altitudinal gradient (Table 1). The cation exchange capacity (CEC) of the soil decreased considerably with altitude. The CEC at the highest altitude was dominated by Al ions occupying 44% of the exchange capacity and the change in Al base saturation percent was exponential from the lowest altitude to the highest altitude (Fig. 9).
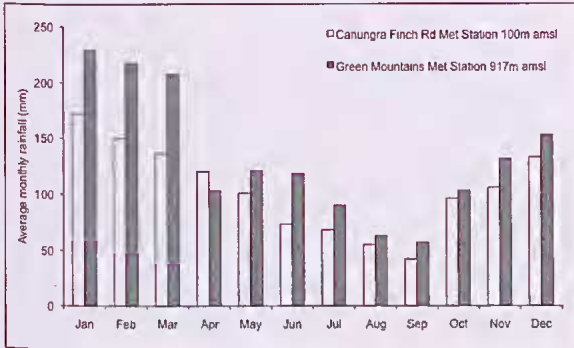
FIG. 7. Long-term monthly rainfall averages within and adjacent to Lamington National Park over the past 92 years at 917 m a.s.l. (Green Mountains Met station) and 100 m a.s.l. (Canungra Finch Road Met station). Source: Australian Bureau of Meteorology.

The macronutrients potassium, calcium and magnesium clearly decreased with altitude and showed a significant difference between altitudes (ANOVA, $P<0.05$) (Table 2). Phosphorous weakly decreased in concentration with increasing altitude but this trend was not significant. Calcium base saturation percent proportionally decreased with increasing altitude as aluminium saturation increased, with the 900 and 1100 m plots exhibiting distinct changes (Fig. 9). Of the macronutrients (N, P, K, Ca, Mg), nitrogen (measured as nitrate and ammonium) did not follow the general trend and increased with increasing altitude (Table 2).

The quantities of trace elements detected in the soil with increasing altitude varied. Sulphur, iron, aluminium and chloride increased with altitude and the differences between altitudes were significant (ANOVA, $P<0.05$) (Table 2). As altitude increased, there was a corresponding, significant decrease in the concentrations of boron, manganese and zinc (ANOVA, $P<0.05$), but no patterns were noted for copper and sodium (Table 2).

Soil moisture. Soil moisture, measured on five sampling occasions (months), consistently increased with increasing altitude (Fig. 10). A significant interaction, however, was found
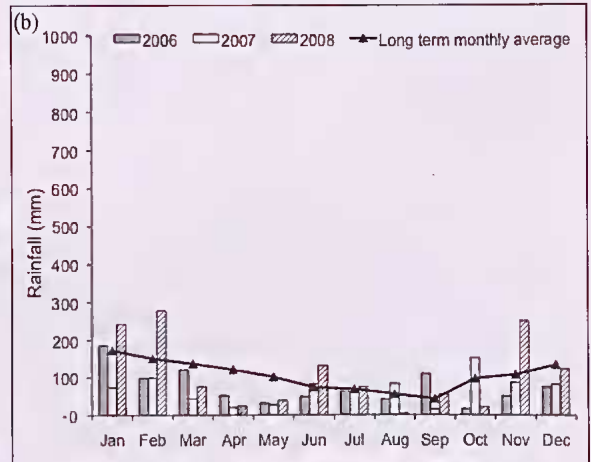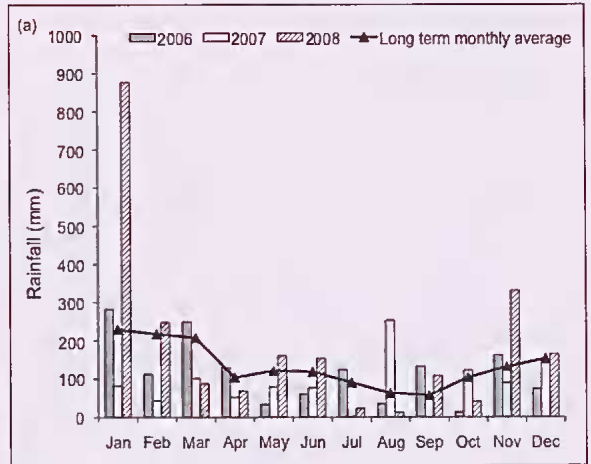

FIG. 8. Monthly rainfall totals collected in or adjacent to Lamington National Park at (a) 917 m a.s.l. (Green Mountains Met station) and (b) 100 m a.s.l. (Canungra Finch Road Met station) over the duration of the IBISCA-Queensland Project (2006-2008) compared with the long-term monthly averages for both sites (see Fig. 7). Approximately 65 % of the monthly totals fell below the long-term average yet rainfall at the two locations followed similar patterns. Data source: Australian Bureau of Meteorology.

between altitude and the sampling month (F = 4.83, $P<0.001$) indicating that, although soil moisture increased with altitude at each month, the differences in soil moisture between each
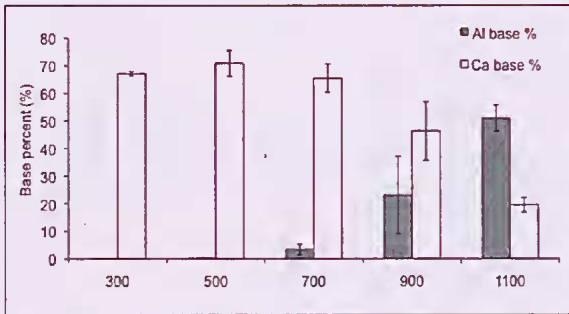
FIG. 9. The increase of aluminium ions in the A horizon from 300 to 1100 m a.s.l. compared to the decrease of calcium ions.

altitude group changed through time. This is apparent in Fig. 10 where it is clear that the 700 and 900 m a.s.l. altitudes tended to track each other through time, while the 1100 m a.s.l. plots experienced a more constant higher level of moisture (Fig. 10).

DISCUSSION

The climate data collected at the five altitudes along the IBISCA-Queensland transect are broadly consistent with previously described changes along altitudinal gradients elsewhere in the world (Bendix *et al.* 2008, Hutley *et al.* 1997, Hodkinson 2005) in demonstrating a general decrease in temperature, an increase in moisture levels and an increase in windiness. Likewise, trends in soil properties are similar to other published accounts of altitudinal gradients (Proctor *et al.* 2007) with decreasing pH and increasing organic matter and soil moisture with increasing altitude. This study has shown, however, that underlying these general trends are more complex climatic responses. These differences have potentially significant implications for the plant and animal communities that exist at different altitudes. Here we discuss the processes at work and the implications for ecosystem function and diversity.

Climate variability with increasing altitude. The average air temperature gradient of 0.75°C 100 m^{-1} along the IBISCA-Queensland transect

is within the moist adiabatic lapse rate range (0.4 –0.8°C 100 m^{-1}) experienced along the eastern Australian seaboard (Sturman & Tapper 2006). Seasonal changes in environmental lapse rates were observed along the IBISCA-Queensland transect with peak austral summer (January) experiencing a moist adiabatic lapse rate of 0.75°C 100 m^{-1} compared to the drier austral winter (August) with a dry adiabatic lapse rate of 1.13°C for every 100 m increasing altitude. As a result, the 1100 m a.s.l. plots experienced colder winters, but effectively more stable temperature conditions than the lower altitudes that have cold overnight winter temperatures, but relatively warm days. Therefore, based on temperature range alone, it could be expected that the cooler but more stable temperature regimes at the 1100 m a.s.l. plots may benefit particular species thus producing a different suite of organisms compared to the 300 and 500 m a.s.l. plots.

The absolute minimum temperatures experienced at the different altitudes did not follow the expected trend of decreasing temperature with altitude (Hutley *et al.* 1997). The 300 and 500 m a.s.l. plots were colder compared to the higher altitudes (Fig. 2) potentially reflecting differences in topographic features between altitudes. Low sun angles in winter deliver the least amount of solar radiation to the Earth's surface (Sturman & Tapper 1996) and therefore southern slopes of escarpments such as both the 300 and 500 m a.s.l. IBISCA-Queensland plots, are most strongly impacted. This enhances colder minimum temperatures at the lower slopes. This is exacerbated by downward movement of air off the surrounding slopes converging to produce zones of cold air drainage (Sturman & Tapper 1996). The understorey at the higher altitude plots (i.e. 700, 900 and 1100 m a.s.l.) appeared to be unaffected by cold air drainage and had absolute minimum temperatures buffered by the canopy. Above 900 m a.s.l., canopy minimum temperatures reflected the average environmental lapse rate of 0.75 °C 100 m^{-1} by becoming colder than the absolute minimums experienced at the plots lowest in the valley.

Moisture is critical for the presence and survival of subtropical rainforests along Australia's east coast, particularly during July, August and September, when Lamington experiences a dry season (Fig. 7). Sources of moisture in rainforests, both tropical and subtropical, include precipitation, wind-blown (near horizontal) rain and cloud or fog droplets collecting on vegetation surfaces. Frequent cloud immersion and fog events are known to occur at altitudes of 800 to 900 m and above (Hutley *et al*. 1997). Hutley *et al*. (1997) determined that the moisture provided by fog deposition accounted for an additional 40% of rainfall collected at a subtropical rainforest site at 1000 m a.s.l. Stripping moisture from fog associated with high relative humidity results

from the cool vegetation acting as a condensation surface. Vegetation, especially in the understorey (because insufficient solar radiation penetrates to warm leaves), produces ideal surfaces for the condensation of water vapour in the form of fog, thereby providing liquid water for biological processes. Low temperatures during winter increase relative humidity and lower dewpoint temperature (Sturman & Tapper 1996) increasing the likelihood of sourcing water from fog stripping (Richards 1996). At the higher altitudes above 900 m, the relative humidity climbed to at least 90% nightly during winter, except for a short time (one week) over mid-winter when relative humidity stayed around 60% (Fig. 4). Lower altitudes have a lower frequency of high relative humidities,
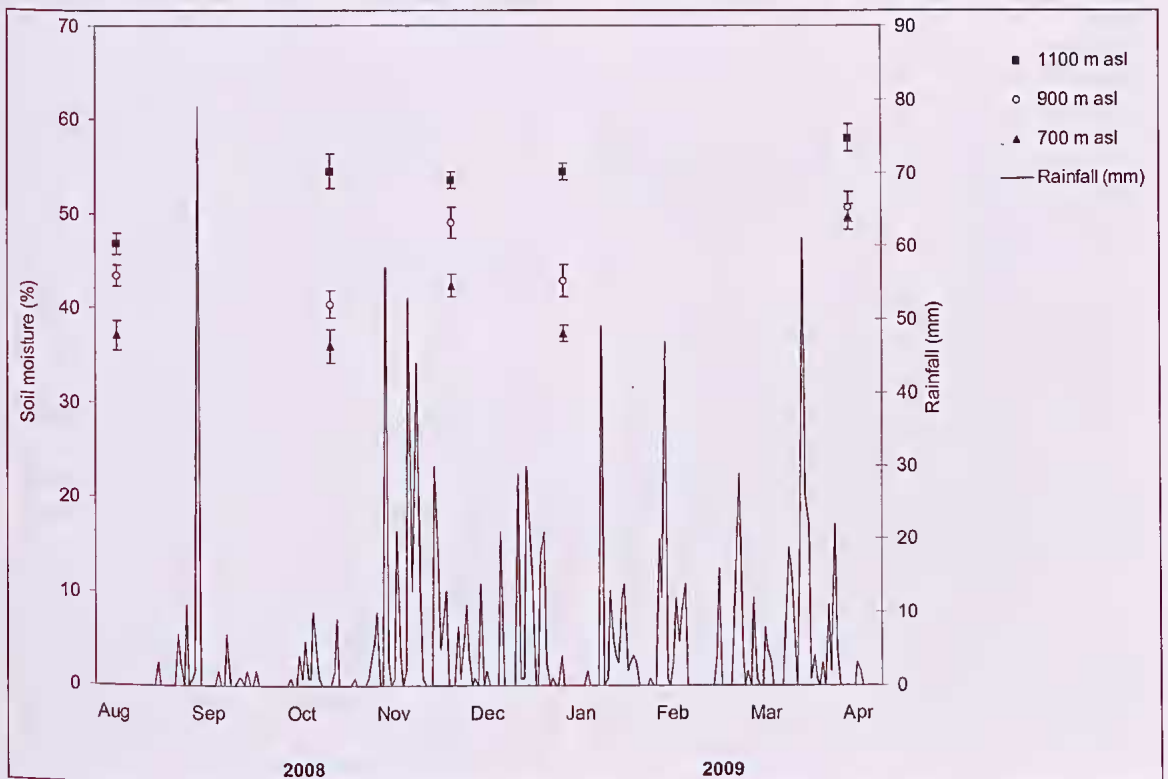

FIG. 10. Mean (± 1 S.E.) soil moisture (%), averaged across four replicate plots, for each of three altitudes (700, 900 and 1100 m a.s.l.) on five sampling occasions (months) at Lamington National Park and daily rainfall (mm), measured at 913 m a.s.l. (O'Reilly's Alert Station; number 40931) over the entire sampling period (source: Australian Bureau of Meteorology).

reducing the opportunity for fog stripping. Water inputs into the higher altitude sites will therefore be greater than those at lower altitudes, impacting on the distribution and composition of communities.

Rainfall totals were greatest at the higher altitude reflecting the effect of topography and meso-scale synoptic patterns. The long-term average annual rainfall measured at 917 m a.s.l. is 1590 mm compared to 1260 mm at an altitude of 100 m a.s.l. (Fig. 8). Topography drives much of this difference, as higher altitudes receive rainfall resulting from orographic uplift. Mountain ranges that face an onshore breeze force the moisture laden winds higher into the atmosphere, condensing the water vapour and often forming cloud and rain (Primack & Corlett 2005). Located on the northern section of the caldera, the higher altitude IBISCA-Queensland plots receive the regular south east trade winds that blow off the Pacific Ocean bringing the moisture associated with a maritime breeze (Sturman & Tapper 1996). This effect is apparent in January 2008 when the 917 m a.s.l. location received over three times as much rainfall as the low altitude location, potentially due to these strong onshore breezes (BoM 2008). In contrast, the two sites received similar rainfall totals in the following month (February 2008) when a meso-scale synoptic event brought widespread rainfall. During this event, an upper level trough moved eastward, combining with moisture laden onshore winds to produce widespread thunderstorms and heavy rain (BoM 2008). This impacted a large regional area whilst not discriminating for altitude.

Meso-scale synoptic events impact moisture delivery, humidity and evapotranspiration. During the drier months, cold fronts move across the country, often bringing strong dry winds (Reeder & Smith 1992) and a reduction in humidity. This results in higher vapour pressure deficits, the deficit between the amount of moisture in the air and how much moisture the air can hold when it is saturated, and the canopy at higher altitudes enduring high evapotranspiration

stress. In contrast, the austral summer brings meso-scale low pressure systems from the southward annual migration of the Inter tropical Convergence Zone (ITCZ) (Sturman & Tapper 1996, Primack & Corlett 2005). This results in extended periods of near saturation at the highest altitudes and a strong tendency for cloud formation and water harvesting via cloud inception (Reeder & Smith 1992). While the lower altitudes are still impacted by meso-scale synoptic patterns, their microclimatic drivers such as local topography and proximity to water sources partially mitigate the full effect of meso-scale drivers (Primack & Corlett 2005).

Wind direction over the observation period changed with altitude reflecting local conditions at low altitude plots and meso-scale synoptic conditions having a greater impact at the more exposed 1100 m plot. Both the 300 m and 500 m plots are located in the bottom of the valley and have topographical features that protect them from winds of meso-scale frontal systems. In contrast, the 1100 m plot is positioned on a south facing escarpment, which is exposed to strong south-westerly to southerly winds associated with cold fronts moving through the forest.

Soil. Soil characteristics strongly influence the distribution and biomass of both plants and animals (Sollins 1998, Peres 2000). Identifying which soil factors are most important is very difficult for there is often a strong correlation between soil texture, drainage, nutrients, and surface topography.

Soil properties depend, in part, on the underlying geology and the rates of weathering of this geology. Basalt geology generally weathers to form relatively nutrient rich clay soils (Churchman *et al.* 1995) but over the long timescales that weathering occurs, many minerals are lost, leaving only quartz and simple structured clays. Cations such as calcium, magnesium, potassium, although derived from weathering of the parent rock, are often either leached out of the soil through water percolation or, such

as phosphorus, form insoluble compounds (Baillie 1996). The high temperatures and rainfall often associated with rainforest areas speed up these processes (Chadwick *et al.* 1999, Hedin *et al.* 2003).

Based on this background, soils of Lamington National Park could be described as being deep, old, highly leached and weathered. They are acidic and infertile, with low levels of plant-available phosphorous, calcium, potassium, and magnesium, and high levels of potentially toxic aluminium. Despite these soil nutrient limitations the undisturbed rainforests rely on the recycling of nutrients through the accumulation of a deep organic matter layer and the rapid uptake of nutrients by a dense mat of roots, mycorrhizal fungi and other soil/litter microorganisms (Cuevas 2001). Despite this heavy reliance on organisms to supply nutrients, the soil characteristics still strongly influence (in part) the distribution of plants and animals (Sollins 1998, Peres 2000).

Changes in soil properties with altitude are influenced strongly by microclimate and topography (Proctor *et al.* 2007, Bendix *et al.* 2008, Wilcke *et al.* 2008, Gerold *et al.* 2008). Generally cooler, wetter conditions at higher altitudes reduce biological activity and increase leaching. Steeper profiles encourage runoff and subsurface movement of water downslope. This manifests in the reduction of weatherable nutrients, such as calcium, magnesium, potassium (Table 2) and a decrease in the cation exchange capacity (CEC) at higher altitudes. These generalised trends are seen in this study with a linear decrease in CEC occurring from 31.7 meq/100g at the 300 m plot to 5.85 meq/100g at the 1100 m plot (Table 1). This range in CEC is comparable to those measured in rainforest A horizon soils in Bolivia (<15 cmol kg^{-1}, Schawe *et al.* 2007), Venezuela (Grimm & Fassbender 1981), and the Ecuadorian Andes (Schrumpf *et al.* 2001).

Associated with the loss of alkaline metal ions (Ca^{2+}, Mg^{2+}, K^+, Na^+) from the soil is a decrease in soil pH. Rainforest soils typically have a low pH (Veneklaas *et al.* 1990, Tanner *et al.* 1998, Grieve *et al.* 1990, Proctor *et al.* 2007) which frequently decreases with increasing altitude (Schawe *et al.* 2007, Wilcke *et al.* 2008, Proctor *et al.* 2007) as seen in the current study (Table 1). Low soil pH in tropical regions is also thought to reflect the acidic nature of organic matter decomposition and root exudates (Schrumpf *et al.* 2001, Hetsch & Honiesel 1976). Arguably, highly acidic soils may decrease plant species richness and soil fauna biomass (Schawe *et al.* 2007). In the present study, soil at the 1100 m plot was highly acidic and this altitude had the lowest plant diversity of the five studied (Laidlaw *et al.* 2011).

Associated with low pH (below 4.8) is the dominance of free aluminium (Primack & Corlett 2005) and therefore a high exchangeable aluminium content which is commonly found in tropical rainforests (Grieve *et al.* 1990, Schulte & Ruhiyat 1998). The availability of aluminium is intensified through soil acidification at higher altitudes as higher moisture levels leach alkaline metal ions (Ca^{2+}, Mg^{2+}, K^+, Na^+) from the soil, further decreasing its pH. This supports the results from IBISCA-Queensland where the highest levels of aluminium were associated with both the lowest levels alkaline metal ions (Table 2) and the highest moisture levels (Table 1). Plants grown in acid soils often suffer aluminium toxicity due to aluminium becoming soluble at low pH thereby impacting on the performance of root systems and manifesting in a variety of nutrient-deficiency symptoms (Mossor-Pietraszewska 1998). In a natural rainforest ecosystem however, the high aluminium content may manifest in a change in floristic composition, with aluminium-tolerant plant species occurring on lowest pH soils.

Accumulation of organic matter at higher altitudes has been noted in other rainforest sites globally and is thought to be associated with frequent water-logging, decreasing temperatures and lower nutrient supply, thereby

reducing organic matter turnover rates due to lower microbial processing (Wilcke *et al.* 2008, Proctor *et al.* 2007). The majority of our results agree with this convention as with increasing altitude we observed increases in organic matter, and soil moisture, a decrease in temperature, reductions in *some* soil nutrients and a decrease in soil acidity. However, we can not be sure that microbial turnover rates are lower at the higher altitudes and therefore responsible for the accumulation of organic matter because this was not specifically tested.

The increase in nitrogen with altitude challenges the argument that high moisture levels and cooler temperatures at the higher altitudes inhibit the microbial turnover of organic matter. This is in contrast to other published studies of rainforest soils along altitudinal gradients (Wilcke *et al.* 2008). Whilst it can be assumed that leaching has been occurring at the study region over the last 20–24 million years, we did not specifically explore the contemporary leaching processes and therefore alternative hypotheses for the high organic matter accumulation at higher altitudes need to be considered.

One such hypothesis is that higher soil organic matter is due to a higher rate of leaf litter fall or a different type of leaf chemistry at the higher altitudes. This is not implausible as the floristic composition of the 1100 m plots markedly differ from those at lower altitudes with an increase in understorey ferns and palms and a canopy dominated by the Gondwanan tree species, *Nothofagus mooreii* (see Laidlaw *et al.* 2011). This tree species is a climate relict, which in Lamington National Park is restricted to a few high altitude locations where temperatures are cooler and moisture levels are higher (Veblen *et al.* 1996). Alternatively, the possibility that ferrolysis may contribute to the destruction of clay minerals should be investigated as an alternative process to leaching (Schawe *et al.* 2007), and may partially explain the higher than expected nitrogen values at the highest altitudes.

To address these anomalies, further studies need to investigate the impacts of leaching on contemporary ecosystem processes by measuring soil moisture over a longer time period and at numerous depths through the soil profile. A greater understanding of the role of microbial turnover at the various altitudes will assist in identifying why organic matter accumulates at higher altitudes and this will be aided by measuring C/N ratios, as well as differences in leaf chemistry which may influence the soil microbial community.

CONCLUSIONS

This study aimed to describe the micro-meteorological properties and soil characteristics associated with an 800 metre altitudinal gradient at Lamington National Park, thereby providing an abiotic context for other IBISCA-Queensland research projects assessing and predicting the patterns of their focus taxa along the gradient. A year-long microclimate monitoring program investigating parameters both in the canopy and understorey at five altitudes is presented and related to changes in soil conditions collected at one point in time. Microclimate data clearly showed that higher altitudes were cooler, had less temperature variability and were moister. Topography is an important driver of patterns of moisture distribution along with gradient, with the higher altitudes intercepting onshore moisture laden breezes allowing for increased moisture capture at these sites via cloud stripping. Topography and aspect at the lower altitude sites influenced local temperatures, particularly in winter, when cold air drainage and low solar radiation levels reduced minimum temperatures below those at higher altitudes. Soil properties generally reflected the climate data, in particular higher moisture and cooler temperatures experienced at the higher altitudes. This produced a general decrease in nutrients and pH with increased altitude. In contrast, soil moisture, organic matter content and soluble aluminium increased with increasing altitude. These trends

are consistent with other studies and suggest that leaching of nutrients caused by higher moisture levels at the higher altitudes is highly probable and that the build up of organic matter may reflect low microbial turnover rates due to cooler, wetter conditions. However further experimentation is required to test this hypothesis.

This study has demonstrated that climate and soil clearly differ with altitude and that these may be important drivers of identified differences between the vegetation of low and high altitude sites (Laidlaw *et al.* 2011). Other taxa studied in the IBISCA-Queensland project may also be directly influenced by these abiotic parameters or indirectly via the impacts they have on vegetation. Under climate change scenarios, atmospheric drying is likely to have a significant impact on the available moisture in this rainforest, impacting both soil and biological processes. The acquisition of new experimental data on the contribution that cloud and fog events have in delivering moisture to soil and vegetation will significantly enhance our ability to simulate changes in spatio-temporal patterns of biota in response to climate change.

ACKNOWLEDGEMENTS

LITERATURE CITED

Baillie, I.C. 1996. Soils of the humid tropics. Pp. 256-286. *In*, Richards, P.W., Walsh, R.P.D, Baillie, I.C. & Greig-Smith, P. (eds), *The Tropical Rain Forest: an Ecological Study*. (Cambridge University Press: Cambridge).

Barry, R.G. 1992. *Mountain Weather and Climate* (2nd ed.). (Routhledge: London/New York).

Beckmann, G.G. & Thompson, C.H. 1976. The soils. Pp. 7-10. *In*, Monroe, R. & Stevens, N.C. (eds), *The Border Ranges, a Land Use Conflict in Regional Perspective*. (The Royal Society of Queensland: Brisbane).

Bendix, J., Rollenbeck, R., Richter, M., Fabian, P. & Emck, P. 2008. Climate. Pp. 63-73. *In*, Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador*. (Springer-Verlag: Berlin Heidelberg).

Bureau of Meteorology. 2008. http://www.bom.gov.au/jsp/ncc/cdio/weatherData/

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J. & Hedin, L.O. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* 397: 491-497.

Chen, I.C., Shiu, H.J., Benedick, S., Holloway, J.D., Cheye, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America* 106: 1479-1483.

Churchman, G.J., Fitzpatrick, R.W. & Eggleton, R.A. 1995. *Clays: Controlling the Environment*. (CSIRO Publishing: Melbourne).

Cuevas, E. 2001. Soil versus biological controls on nutrient cycling in terra firme forests. Pp. 53-67. *In*, McClain, M.E., Victoria, R.L. & Richey, J.E. (eds), *The Biogeochemistry of the Amazon Basin*. (Oxford University Press: Oxford).

FAO. 1998. *World Reference Base for Soil Resources*. (Food and Agriculture Organization of the United Nations: Rome).

Gerold, G., Schawe, M. & Bach, K. 2008. Hydrometeorologic, pedologic and vegetation patterns along an elevational transect in the montane forest of the Bolivian Yungas. *Erde* 139: 141-168.

Graham, B.W. 2001. *Tweed Volcanic Region: 360 Million Years Ago to the Present Day*. (B.W. Graham: Tweed Heads).

Grieve, I., Proctor, J. & Cousins, S. 1990. Soil variation with altitude on Volcan Barva, Costa Rica. *Catena Supplement* **17**: 525-534.

Grimm, U. & Fassbender, H.W. 1981. Ciclos bioquimicas en um ecosistema forestal de los Andes Occidentales de Venezuela. I. Inventario de las reservas organicas e minerales (N, P, K, Ca, Mg, Fe, Al, Na). *Turrialba* **31**: 27-37.

Hedin, L.O., Vitousek, P.M. & Matson, P.A. 2003. Nutrient losses over four million years of tropical forest development. *Ecology* **84**: 2231-2255.

Hetsch, W. & Hohiesel, H. 1976. Standorts-und Vegetationsgliederung in einem tropischen Nebelwald. *Allgemeine Forst- und Jagdzeitung* **147**: 200-208.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* **80**: 489-513.

Hutley, L.B., Doley, D., Yates, D.J. & Boonsaner, A. 1997. Water balance of an Australian subtropical rainforest at altitude: the ecolological and physiological significance of intercepted cloud and fog. *Australian Journal of Botany* **45**: 311-329.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55(2)**: 235-250.

Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* **55(2)**: 271-290.

McDonald, W.J.F. & Whiteman, W.F. 1979. *Moreton Region Vegetation Map Series: Explanatory Booklet for the Murwillumbah Sheet.* (Botany Branch Qld Department of Primary Industries: Brisbane).

Morand, D.T. 1996. *Soil landscapes of the Murwillumbah-Tweed Heads 1:100 000 sheet.* (Department of Land and Water Conservation: Sydney).

Mossor-Pietraszewska, T. 1998. Effect of aluminium on plant growth and metabolism. *Acta Biochimica Polonica* **63**: 673-686.

Northcote, K.H. 1979. *A Factual Key for the Recognition of Australian Soils.* (Rellium Technical Publications: Glenside).

Peres, C.A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* **14**: 240-253.

Primack, R.B. & Collet, R. 2005. *Tropical Rain Forests: an Ecological and Biogeographical Comparison.* (Blackwell Publishing: Cornwell).

Proctor, J., Edwards, I.D., Payton, R.W. & Nagy, L. 2007. Zonation of forest vegetation and soils of mount Cameroon, West Africa. *Plant Ecology* **192**: 251-269.

Rayment, G.E. & Higginson, F.R. 1992. *Australian Laboratory Handbook of Soil and Water Chemical Methods.* (Inkata Press: Melbourne).

Reeder, M.J. & Smith, R.K. 1992. Australian spring and summer cold fronts. *Australian Meteorology Magazine* **41**: 101-124.

Richards, P.W. 1996. *The Tropical Rain Forest.* (Cambridge University Press: Cambridge).

Schawe, M., Glatzel, S. & Gergold, G. 2007. Soil development along an altitudinal transect in a Bolivian tropical montane rainforest: podzolization vs. hydromorphy. *Catena* **69**: 83-90.

Schrumpf, M., Guggenberger, G. & Valarezo, C. 2001. Tropical montane rain forest soils. *Die Erde* **132**: 43-59.

Schulte, A. & Ruhiyat, D. 1998. *Soils of Tropical Forests Ecosystems: Characteristics Ecology and Management.* (Springer-Verlag: Berlin Heidelberg).

Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* **79**: 23-30.

Stevens, N.C. 1976. Geology and landforms. Pp. 1-6. *In*, Monroe, R. & Stevens, N.C. (eds), *The Border Ranges, a Land Use Conflict in Regional Perspective.* (The Royal Society of Queensland: Brisbane).

Sturman, A.P. & Tapper, N.J. 2006. *The Weather and Climate of Australia and New Zealand.* (Oxford University Press: Melbourne).

Tanner, E., Vitousek, P. & Cuevas, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* **79**: 10-22.

Veblen, T.T., Hill, R.S., & Read, J. (eds) 1996. *The Ecology and Biogeography of Nothofagus forests.* (Yale University Press: New Haven, London).

Veneklaas, E. & van Ek, R. 1990. Rainfall interception in two tropical montane rain forests, Columbia. *Hydrological Processes* **4**: 311-326.

Wilcke, W., Yasin, S., Schmitt, A., Valarezo, C. & Zech, W. 2008. Soils along the altitudinal transect and in catchments. Pp. 75-85. *In*, Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador.* (Springer-Verlag, Berlin Heidelberg).

Williams, S.E., Bolitho, E.E. & Fox, S. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**: 1887-1892.

Willmott, W. 2004. *Rocks and Landscapes of the National Parks of Southern Queensland.* (Geological Society of Australia (Queensland Division): Brisbane).